# Occurence of the introduced black rat (*Rattus rattus*) and its potential effects on endemic rodents in southeastern Madagascar

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Academic dissertation

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The thesis is based on the following articles which are referred to in the text by their Roman numerals:

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II Lehtonen, J.T., Rasataharilala, V., Dehgan, A. & Niemelä, J.: Effects of rainforest fragmentation on rodents in southeastern Madagascar

III Rita, H. & Lehtonen, J.T. Explanatory framework (EFRA): a non-statistical statistical tool for ecologists – Case: habitat use of black rat in Madagascar

IV Miljutin, A. & Lehtonen, J.T. 2008: Probability of competition between the introduced and endemic rodents in Madagascar: an estimation based on morphological traits. – Estonian Journal of Ecology 57 (2): 133.52.

## Contributions

The following table shows the major contributions of authors to the original articles or manuscripts (referred to as I-IV)

| | I | II | III | IV |
|---|---|---|---|---|
| Original idea | OM, JN, JTL | AD, JTL, JN | HRi, JTL | JTL, AM |
| Study design | JTL, OM | JTL, AD | JTL, HRi | AM |
| Data collecting | JTL, HRa, OM | JTL, VR | JTL, VR | AM, JTL |
| Analysis | JTL, HRi | JTL | JTL, HRi | AM |
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# Abstract

Native faunas and floras are especially susceptible to negative effects of invasive alien species in islands. The world´s fourth largest island, Madagascar, has very unique biota with high level of endemism. The black rat, *Rattus rattus,* is claimed to cause more extinctions of insular vertebrates than any other introduced rodent in the world. On Madagascar, *R. rattus* is suggested to competete with native rodents belonging to the endemic subfamily Nesomyinae. Extensive deforestation and fragmentation also threatens Malagasy forest-dwelling species.

The aims of this thesis were to 1) study the occurence of native and introduced species and the different kind of factors determining occurence in southeastern Madagascar and 2) help to target future studies by estimating which native rodents are the most potential competitors with introduced rodents on Madagascar.

Habitat use data of black rat and endemic rodents were collected both in fragmented and in unfragmented forest in Ranomafana National Park in southeastern Madagascar. A total of 698 rodent individuals were captured in 6204 trap nights. Logistic and Poisson regression models were used to determine the factors that influence the presence and abundance of rodent species and to investigate how sensitive one variable can be to other variables in regression models. This led to the introduction of a new approach called 'explanatory framework based regression analysis'(EFRA) which rests on the social science –based elaboration technique. EFRA enables systematization of the link between ecological knowledge and statistical analysis. From the point of it multicollinearity is more source of information than a problem for data analysis.

The abundance of *R. rattus* increased with increasing forest disturbance. The spread of *R. rattus* was suggested to be associated with deforestation but not directly with fragmentation. It is not surprising when remembering that *R. rattus* utilizes open areas too. The measured value of the size of the fragment can be viewed as an index capturing certain features of the forest fragment.

For Malagasy native rodents, clear-cutting is disastrous and forest fragmentation may have a diminishing effect on populations of *Nesomys audeberti*. However, none of the native species was more abundant in un-logged than in selectively logged forest. There was no evidence that *Eliurus webbi* suffers directly from forest fragmentation but it may be more susceptible to interactions with *R. rattus* in fragments than in continuous forest.

In the last paper, the comparison of morphological measurements leads to the conclusion that there is a high probability of competition between introduced *R. rattus* and the following native taxa: all species of Nesomys, larger semiarboreal Eliurus species (e.g. *E. tanala, E. webbi*), and especially *Gymnuromys roberti*.

# SUMMARY

# Summary

## 1. Introduction

### 1.1 Invasive alien species

It is widely reported that invasive alien species are one of the most important threats to species extinctions worldwide (Vitousek et al. 1996, 1997; Wilcove et al. 1998, Mack et al. 2000, Clavero & Garcia-Berthou 2005) and particularly on islands (Sax & Gaines 2008, Fordman & Brook 2010). Although it has been criticized that many researches supporting invasion as a cause of extinctions are speculative and based upon limited data (Gurevitch & Padilla 2004), there are several examples where invasive species have driven local species to extinctions or in other ways outstandingly altered ecosystems. One of the best known examples is Guam's island where the accidental introduction of the brown treesnake around 1950 has caused the extinction or dramatic population decline of ten of 13 native bird species, nine of twelve reptile species, and all three mammal species (Fritts & Rodda1998).

Invasive alien animal species can drive other species to extinction in three ways: 1) by direct competition, 2) by predation, and 3) by spreading parasites or pathogens. There are surprisingly few instances in which indigenous species have been driven to extinction by direct competition with invasive species (Davis 2003). Rather, numerous extinctions or replacement of long-term resident species have been suggested to be caused by the introduction of new parasites and pathogens (McCallum and Dobson 1995, Combes 1996, Daszak et al. 2000, Davis 2003, Tompkins et al. 2003) or predators (e.g. Savidge 1987, Fritts & Rodda1998, Thibault et al. 2002). Gurevitch & Padilla (2004) examined the IUCN Red List database and noticed that 37 animal species were threatened by direct effects of competition, 58 species by pathogens or parasites, and 113 species by predation.

According to the enemy release hypothesis, invaders can get an advantage over their competitors when they lose a considerable part their enemies such as parasites, pathogens, predators, and herbivores in their new location (Keaney & Crawley 2002, Mitchell & Power 2003, Torchin et al. 2003, Prenter et al. 2004, Drake 2005). Torchin et al. (2003) analysed parasitological studies of 26 invasive animal species from seven taxa and demonstrated that the number of parasite species found in exotic populations is roughly half that found in their native populations. However, introduced species may also get harmful parasites from native species.

Most extinctions facilitated by invasive alien species have been on islands as opposed to mainland (Sax & Gaines 2008). Island native faunas and floras are especially susceptible to negative effects of exotic species because of low species richness, isolation, evolution under relatively stable conditions, and decreased competitive ability and predator awareness (Williamson 1989). Forest disturbance may also facilitate the invasion of undesirable non-native species (e.g. Diamond et al. 1987, Kesavaraju et. al. 2008, Corlett 2010, Rickart et. al. 2011). Logging may cause very long-lasting effects. In Madagascar logged rainforest areas never recovered native plant species diversity because of the dominance of nonnative plant species (Brown and Gurevitch 2004).

### 1.2. Introduced rodents on islands

Several rodent species have been introduced on islands, many of which have negative effects on other species (Simberloff 2008). The four species that are most commonly implicated to cause negative ecosystems impacts include the house mouse (*Mus musculus*), the black rat (*Rattus rattus*), Norway rat (*R. norvegicus*), and the Pacific rat (*R. exulans*) (Towns et al. 2006, Harris 2009). All of these except *R. exulans* is present on Madagascar (Duplantier & Duchemin 2003). Three species of rats have occupied 90 % of the world's major islands (Oppel et al. 2011). Towns et al. (2006) reviewed the global literature on the effects of introduced rats on island flora and fauna and found that black rats and Norway rats affected mostly seabird and landbird species and were the only species which also affected mammals. However, the fact that introduced rodents are known to cause more negative effects on insular birds than on rodents is partly because insular birds have been studied wider than rodents (Harris 2009).

Black rats are claimed to cause the largest number of declines or extinctions of insular vertebrate species (60), including five species of rodents (Towns et al. 2006). Harris (2009) found three rodent species more and suggested the reason that *Rattus rattus* is considered in the majority of conservation problems is due to its extensive distribution and ecological plasticity. As most of the eight extinction cases of rodents happened more than hundred years ago, they are not properly studied and an extinction mechanism is not proven.

According to Harris (2009) the *Rattus rattus* –caused extinction mechanism is best supported in Christmas Island where two rodent species disappeared within ten years after the introduction of a blood parasite trypanosome infected *R. rattus*; heavy trypanosome infection was also recorded in native rodents (Pickering & Norris 1996). In Madagascar, only few trypanosomes were found in native *Nesomys rufus* rodents and they differed morphologically from those found in *Rattus rattus* (Laakkonen et al. 2003a, 2003b). However, it was unclear if the few trypanosomas found in Malagasy rodents were spread by *Rattus* and whether a lethality effect was the reason for the lack of *Trypanosoma lewisi* –like trypomastigotes in Malagasy rodents.

In most other extinction cases, the loss of native species has quickly followed the introduction of *R.rattus* but an extinction mechanism is more or less speculative. The

disappearance of two rodent species, *Rhagamys orthodon* in Corsica and Sardinia islands (Wilson 1991) and *Oryzomys nelson* in Mexico (Vigne and Valladas 1996), has been suggested to be caused by competition with *R. rattus*. However, it is not very probably that the extinction can be explained by a single factor. Vigne and Valladas (1996) discussed that *R.rattus* may increase sensitivity of native rodent species to environmental change.

### 1.3. Effects of human disturbance on Malagasy biota

Madagascar is the fourth largest island in the world and separated from the African continent by the 400 km wide Mozambique Channel. It isolated from the African continent about 160 million years ago and from India about 80 million years ago (de Wit 2003).

Biota of Madagascar is very unique as species-level endemism reaches 82 % in vascular plants (Callmander et al. 2011). For animals the proportion is usually even higher, for example 96 % in dung beetles (Wirta 2009). All non-introduced land mammals are endemic (Goodman et al. 2003). Madagascar is one of the world's hotspot areas with 3.2 % and 2.8 % of the total global endemic plants and vertebrates, respectively (Myers et al. 2000, de Wit 2003). Almost 50 % of the world's chameleon species are seen only on Madagascar. Typical to Malagasy fauna is also a lack of many taxa. There are no native canids, felids, and ungulates except for three extinct pygmy hippopotami species.

Human colonization history on Madagascar is a disputable topic. Gommery et al. (2011) suggested that the cut marks of hippopotamus bones dated to approximately 2000 BC is the oldest evidence of human presence on Madagascar. However, according to geographical screening of Malagasy and Indonesian human genetic variation, Madagascar was settled approximately 1200 years ago (Cox et al. 2013). Regardless of whether the moment of human colonization was before or after the Common Era, it has been followed by several species extinction: 17 species of large-bodied lemurs, 3 species of hippopotami, the elephant bird, and giant tortoises (Burney et al. 2004). However, the causes of these extinctions are complex, and the role of humans in the extinction process is probable but not proven.

The forest decline is unambiguously human-mediated on Madagascar. The most important reason for deforestation on the island is charcoal production and the needs of agriculture, which usually implies a slash and burn -culture (Green & Sussman 1990). In Madagascar, slash and burn culture is called ´tavy´ and is illegal. Estimates of deforestation indicate that 50–80 % of primary vegetation has already been lost on Madagascar (Green & Sussman 1990). The highest estimates are opposed with the argument that originally the highland areas were covered by wooded grassland instead of continuous forest (Burney 1997). Puhakka (2012) studied the tropical rainforest corridor between two national parks, Ranomafana NP and Andringitra NP, in south-

eastern Madagascar and found that the deforestation rate in the area varied between 1.2 % (1990–2000) and 1.5 % (2000–2005).

Deforestation can assist the spreading of invasive species, too. In Ranomafana NP, the colonization of invasive plant species in forests clear-cut or selectively logged in the past prevented return of native plant species even after 150 years (Brown & Gurevitch 2004).

Forest fragmentation is also an acute problem in Madagascar. In 2000, almost half of Malagasy forest existed in fragments less than 500 $km^2$ (Harper et al. 2007). This means that more and more animals and plants are living close to forest edge as over 80 % of forested area was less than one kilometre from the edge of forest (Harper et al. 2007). After reviewing the response of several different plant and animal taxa to anthropogenic disturbance, Irwin et al. (2010) concluded that forest disturbance usually decreases endemic species diversity in Madagascar, but different species and other taxa have very divergent reactions.

### 1.4. Native rodents of Madagascar

All 27 species (9 genera) of Malagasy native rodents belong to the same endemic subfamily Nesomyinae (Soarimalala & Goodman 2011). Based on a phylogenetic approach, Jansa et al. (1999) suggested that Madagascar was colonizated by nesomyines via a single invasion; nesomyines later dispersed from Madagascar to Africa. However, the placement of nesomyines in murid rodent evolutionary history has afterward been guestioned by other molecular studies (Steppan et al. 2004, Jansa & Weksler 2004), and their monophyletic origin is not clearly confirmed or rejected.

There is a great variety in size among the species of nesomyine rodents. The body weight varies in Nesomyine from 20 to 1300 g, and the head and body length vary from 80 to 345 mm (Carleton, Goodman, 1998; Garbutt, 2007). The contemporary fauna of Nesomyinae contains one very large species (*Hypogeomys antimena*), four small species with the head and body length less or around 100 mm (*Eliurus minor, Macrotarsomys bastardi, Monticolomys koopmani*, *Voalavo gymnocaudatus*), and 19 species of medium size with head and body length in adults between 120–250 mm. The size of introduced rodents are comparable with the two last groups. *Mus musculus* is about the size of small nesomyines, while two *Rattus* species are comparable with larger medium sized nesomyines. Therefore, most of the Malagasy rodent species are about the same size as introduced ones.

The most species-rich genus among Malagasy rodents is tuft-tailed rats, Eliurus, including twelve nocturnal and arboreal species (Goodman et al. 2009). Representatives of Eliurus have been found in all natural forest types in Madagascar (Goodman et al. 2003). Red forest rats, Nesomys, are the only diurnal rodents in Madagascar. All three species of Nesomys are terrestrial. Two of these species occur in the eastern rainforest of Madagascar. *N. audeberti* prefers lower elevations than *N. rufus* (Ryan et al. 1993; Goodman & Carleton 1999). Altitude is known to affect the presence and abundance

of Malagasy rodent species (Goodman et. al. 1996; Goodman and Carleton 1996, 1998; Carleton & Goodman 2000), but other factors influencing their habitat use have been analysed in more detail by a few studies only (Stephenson 1995, Ramanamanjato & Ganzhorn 2001, Ganzhorn 2003).

The subfossils of Malagasy small mammal fauna is very poorly studied and only three nesomyine rodent species are known to be extinct so far: *Brachytarsomys mahajambaensis, Hypogeomys australis,* and *Nesomys narindaensis* (Goodman & Rakotondravony 1996, Mein et al. 2010). They all have been recovered in upper pleistocene or Holocene deposits. Therefore, the fossil data does not give reason for speculation of possible nesomyine extinction caused by *Rattus rattus.*

Only a few studies have addressed the effects of fragmentation and deforestation on the eastern small mammal fauna in Madagascar. Research conducted in the montane humid forests of the Central High Plateau demonstrated that endemic rodents were rare at same time when the introduced *R. rattus* was abundant in forest fragments (Ganzhorn et al. 2003). In littoral forests of southeastern Madagascar, Ramanamanjato and Ganzhorn (2001) found that the endemic rodent *Eliurus webbi* was sensitive to fragmentation, but they found no effects in its association with *R. rattus*.

### 1.5. Introduced rodents on Madagascar

Contrary to many other islands, not many invasive alien animal species have occupied Madagascar. If domestic animals are not included, eight introduced mammal species are living in Madagascar (Garbutt 2007). Three of these are rodents: *Mus musculus, Rattus norwegicus,* and *Rattus rattus.*

The first archaeological record for Rattus on Madagascar was found in the northwest part of the island from the 11th-14th century (Rakotozafy 1996, Radimihilahy 1997). However, according to mitochondrial DNA analyses, the colonization of *Rattus rattus* probably happened much earlier but not prior to human arrival (Tollenaere et al. 2010). The sequences of Malagasy *Rattus rattus* were most closely related to the sequences found in Oman (Tollenare et al. 2010), suggesting that the Arabian Peninsula is the strongest candidate for the origin of *R. rattus* colonization on Madagascar. Tollenaere's et al. (2010) observations support the hypothesis of a single colonization of Madagascar. The population of *R. rattus* seems to have expanded rapidly first in coastal areas and later in the central highlands.

Now *Rattus rattus* has invaded most of Madagascar (Goodman 1995). In many study sites in Madagascar (e.g. in Andringitra Strict Nature Reserve), *R. rattus* has not only been found close to human habitation but also deep within undisturbed forests (Goodman & Carleton 1996). Goodman (1995) has suggested that the invasion of *R. rattus* may threaten endemic rodent species on Madagascar. This is supported by two observations: 1) there is an overlap in food composition of *R. rattus* and some nesomyine rodents (Goodman and Sterling 1996), and 2) the abundance of *R. rattus* at certain sites is much higher than that of the native rodents (Stephenson 1993,

Goodman et al. 1996, 1997). The biggest proportion of *R. rattus* has been observed in the humid forest of Montagne d'Ambre at 1350 meters in elevation where all 104 captured rodents, with the exception of one individual, were *Rattus rattus* during 750 trap-nights (Goodman et al. 1996) even though this altitude is where native rodent species richness is generally high in Madagascar. However, Ganzhorn (2003) couldn't find evidence for competition between *R. rattus* and native small mammal fauna in dry deciduous forest in Western Madagascar. No experimental studies testing the competition hypothesis have been done in Madagascar.

The origin of Norway rat, *Rattus norvegicus*, is in southeastern Siberia and northern China and therefore it is not very common in tropical countries (Musser & Carleton 1993). In Madagascar, *R. norvegicus* occurs only in towns of cenral highlands and harbours but some single individuals have also been captured elsewhere (Duplantier & Duchemin 2003). A mitochondrial study showed that the house mouse in Madagascar originated from the Arabian Peninsula in a single colonization (Duplantier et al. 2002). The house mouse is found in almost all kinds of habitats except for closed forests (Langrand & Goodman 1997; Rakotondravony & Randrianjafy 1998; I).

## 2. Aims of thesis

It was necessary to obtain more information about the ecology of *Rattus rattus* on Madagascar because: 1) *Rattus rattus* is claimed to have caused more extinctions of insular vertebrate species than any other introduced rodent in the world (Towns et al. 2006), 2) black rats are suggested to competete with native rodents on Madagascar even though there is little empirical evidence to support this claim (Goodman 1995), and 3) *R. rattus* is not only a problem for conservation, but it is one of the most damaging agricultural pests and an important transmitter of human diseases (e.g. plague, hantaviruses and intestinal bilharziasis) in Madagascar (Duplantier & Rakotondravony 1999)

Unlike many other tropical areas in the world, *R. rattus* has not only been found close by human habitation, but also deep in undisturbed forest (Goodman & Carleton 1996). However, during our first studies (I) in Ranomafana National Park in 1996 and 1998, we caught *R. rattus* and *Mus musculus* only close by human habitation. It was possible that in Ranomafana *R. rattus* was just in the beginning of its expansion to primary forest or it had not succeeded in doing so. Thus, the surrounding of Ranomafana National Park proved to be an interesting area to study the occurrence of *R. rattus.* All types of ecological data about rodents in the area was needed because the national park was established in 1991 and a new research station, Centre Valbio, was inaugurated in 2001. Only two papers were published about the rodents of Ranomafana before our study (Carleton and Schmidt 1990, Ryan et al. 1993).

Because the knowledge of Malagasy rodent ecology was scarse, it was good to start to study the presence and abundance of rodent species and the different factors de-

termining them (I, II and III). As *Rattus rattus* is a human-mediated species, special attention was paid to the effects of human disturbance on the occurrence of species. In chapters I, II, and III the aims were 1) which rodent species co-exist (I, II)?, (2) what are their species-specific habitat utilisation patterns (I, II)?, and (3) how does anthropogenic habitat disturbance and fragmentation affect the rodent community (I, II and III) ?

When analyzing the occurence data we noticed how sensitive one variable can be to other variables in regression models. In the methodological chapter (III), the goal was to introduce the social science -based elaboration technique into ecological research and to show how elaboration enables better utilization of our ecological knowledge in statistical data analysis. As the habitat use of *R. rattus* on the fragmented forest areas was used as an example, the second aim was to get a more in-depth interpretation about the effect of forest fragmentation on the presence of *R. rattus* at the same time.

The competition between native and introduced rodents on Madagascar is very difficult to study without a good idea about target species. The last goal of this thesis was to help to target future studies by estimating which native rodents are the most potential competitors with introduced rodents on Madagascar (IV). This estimation would hardly be done on the basis of scarse ecological data. Rather, the degree of ecomorphological similarity between introduced and nesomyine rodents was used.

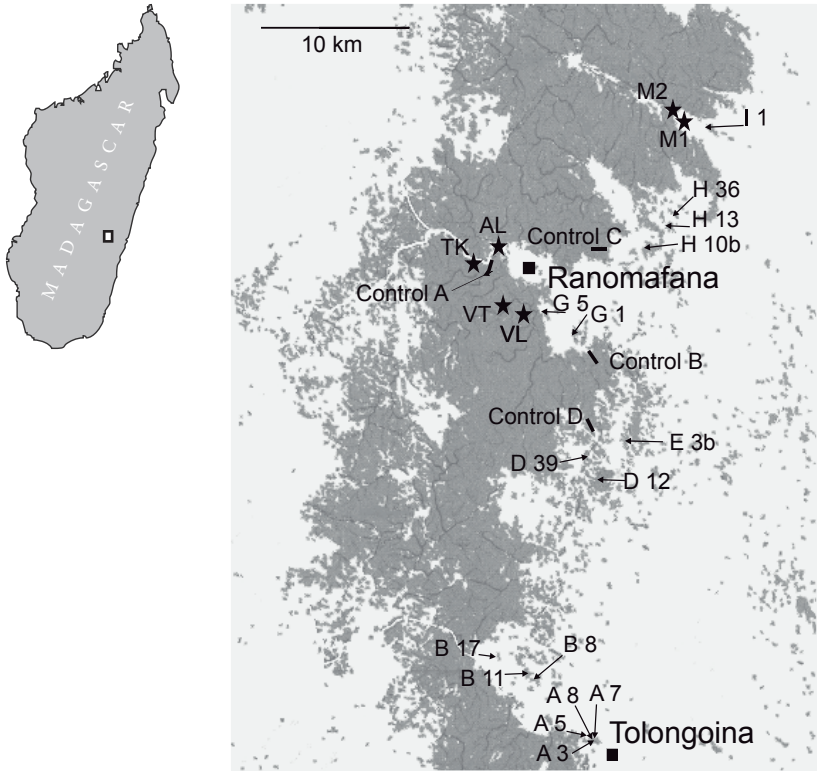
The original idea of the thesis was also to examine whether rats, mice, and native rodents share any endoparasites. We collected parasitogical data and some parts of it have already published (Laakkonen et al. 2003a, 2003b; Haukisalmi et al. 2010). Because we found altogether at least twelve new endoparasite species and only five of them (Durette-Desset et al. 2002a, 2002b, 2007) have been described so far, we passed the parasitological study in this dissertation.

## 3. Material and methods

### 3.1. Study area

The study was conducted in the Ranomafana National Park (RNP: 21 × 16′, 47 × 20′) in southeastern Madagascar, in its 3 km wide surrounding peripheral zone (I, II and III), and in the fragmented area (II, III) on the eastern and southeastern side of the RNP (Map 1). The protected core area of RNP, created in 1991, covers 43 500 ha of relatively undisturbed lowland rain forest, cloud forest, and high plateau forest (Grenfell & Robinson 1995). The altitudinal gradient ranges from 500 meters to 1500 meters. Over 25 000 residents are living in more than 100 villages in the peripheral zone of the RNP.

Six monitoring study sites were visited between 15 September and 29 November 1996, 1998, 1999, and 2000. Three of these sites were located in primary forests




*Map 1. In Chapter I trapping grids were situated in six annual monitoring sites (stars, M= Miaranony, AL = Ambatolahy, TK = Talatakely, VT = Vatoharanana, VL = Valohoaka) and three additional lines (close by monitoring sites but not shown in the map). In Chapter II and III trapping grid were situated in 12 forest fragments (arrows) and four control sites. The dark grey areas represent the remaining forest cover according to the satellite photos taken in 1997.*

(i.e., unlogged or slightly selectively logged forest): Vatoharanana (VT), Valohoaka (VL), and Miaranony II (M2). Another three study sites were in secondary forests (i.e., heavily logged forest): Talatakely (TK), Ambatolahy (AL), and Miaranony I (M1) (Map 1) . For further information about the monitoring study sites see Chapter I, Wright (1997). Each of the six study sites included 10 (M1 and M2) or 12 (other sites) trapping plots. In this thesis the monitoring data of years 1996 and 1998 is used in Chapter I. The monitoring data of all other years are shown in Table 1 but are not used in other parts of the thesis. In addition to the monitoring plots, 44 extra trapping plots were studied in 1998. These trapping plots were placed along three lines between the primary forest areas and areas where *R. rattus* was known to occur. In total, the data of 112 trapping plots was used in Chapter I.

The study fragments (II, III) were situated in a 40 km long and 5 km wide zone between 600 meters and 1000 meters in elevation (Map 1). Field studies were carried

out in 2000, and satellite photos taken in 1997 were used to measure fragments. There were approximately 240 forest fragments ranging in size from 0.5 to 200 ha in area in 1997. The habitat matrix between the forest fragments consists of agricultural fields, grasslands, and villages. The loss rate of forest patches has been alarming in the corridor area between the RNP and the Andringitra NP: the number of patches decreased 54 % in 1990–2005 (Puhakka 2012).

### 3.2. Trapping methods

We used trapping grids in all studies but trapping grids were different in Chapter I than in Chapters II and III. Each trapping plot was a square measuring 20 x 20 m in Chapter I and 15 x 15 m in Chapters II and III. Live trap types were also different. Only one big live trap was in every corner in Chapter I whereas two live traps were utilized in every corner in Chapters II and III (see more details in I and II). Traps were in the field three nights in Chapter I and five nights in Chapter II and III. In the fragmentation study (II, III), a total of 95 trapping grids were established in 20 study sites (16 forest fragments ranging from 0.5 to 170 ha and four control sites in unfragmented forests). All study grids were situated at an elevation of 650–910 m.

In all trapping for this thesis (I,II, III), live traps were baited daily, on afternoons, with fresh banana slices and peanut butter. The traps were checked in the morning beginning at 07:00 h. Captured animals were sexed, examined for reproductive condition, weighed, and measured. All captured individuals of *Rattus rattus* were sacrificed, but most of the endemic species were released after measuring and earmarking. In order to study endoparasites or preserve voucher specimens, some representatives of nesomyine rodent species were collected.

### 3.3. Habitat variables

Twelve habitat variables of forest and landscape structure were the same at all trapping grids (I, II, III): canopy cover; fallen log density; herbaceous cover; liana stem density; overstory tree height; altitude; and slope and distances from a building, field, human habitation (distance from the grid to nearest house, permanent satellite campsite, or to a recently cultivated field), forest edge, and stream. All trapping plots were also divided into four categories of human disturbance: (1) secondary bush, (2) heavily logged forest, (3) selectively logged forest, and (4) pristine forest. If the exact logging history of the trapping plot was not known, it was estimated by the occurrence of the following plant indicator species of forest disturbance: *Clidemia hirta*, *Dombeya* sp., *Harunga madagascariensis*, *Psidium cattleianum*, *Ravenala madagascariensis* (Lowry et al. 1997). In addition to these variables, the area of the fragments and the distance of a fragment from continuous forest and from the three nearest neighboring patches were also measured in fragmented area (II, III). All habitat variables were measured by same person.

### 3.4. Data analyses of habitat variables

Logistic regression was used to examine the effect of various habitat variables on the presence of the rodent species in trapping grids (I,II, III). Explanatory variables affecting the abundance of rodent species were modeled by Poisson regression (I). Only those zero observations that according to the logistic model had at least 30 % probability of species presence (Lindenmayer et al. 1991) were included in the abundance analysis. Without the elimination of some of the empty trapping grids extreme variable values which only indicate presence but not abundance of the studied species would have been included. Finally, the best-fit models were tracked by the forward stepwise procedure (I).

The logistic models developed in Chapter I were tested for predicting the presence of rodent species in the fragments and in continuous forest in Chapter II. Error rate (an estimate of the number of incorrect predictions), sensitivity (a measure of the ability of the model to predict the presence of studied species at a grid), and specificity (the ability of the model to correctly predict that studied species will not occur on a given square) were calculated as provided by Lindenmayer et al. (1991).

Although best-fit models were used in Chapter I, problems with using them were later realised. Mac Nally (2000) highlighted that best-fit models can be appropriate when the purpose of the modelling is to achieve a predictive model, but because of multicollinearity problems you can not use it for explaining causality. Predictive models can occasionally be useful in conservation biology, for example, if you have to predict distribution of endangered species for the purpose of protected area planning. However, drawing inferences about the causality of variables is often of more interest in classical ecology as well as in applied ecology (Mac Nally 2002). For example, if you have to prevent introduced species from invading more, you have to know not only where it is going to invade but also why it is going to invade to a certain site. Macnally's (2002) solution to multicollinearity problems was hierarchical partitioning with using randomization of the data matrix. However, hierarchical partitioning is mostly a technical tool. Austin (2002) claimed that neglect of ecological theory is a limiting factor in the application of statistical modelling in ecology. We relied on ecological knowledge with utilizing the idea of elaboration (see Box 1, III).

In Chapter III, the idea of elaboration is applied to logistic regression models of habitat use by black rat in fragmented areas. We call our approach 'explanatory framework based regression analysis'(EFRA), which enables systematization of the link between ecological knowledge and statistical analysis. It is important to take into consideration how the explanatory variables are related to each other which is often reflected as multicollinearity. The starting point for EFRA is that multicollinearity is more a source of information than a nuisance to data analysis as often seen in ecological research.

When using the EFRA approach, the interplay between the different explanatory variables and the ecological importance of the coefficient of fragment size were explored. In addition to fragment size, other variables were included in the logistic re-

gression model and the resulting changes in the estimated values of the coefficient of fragment size were recorded. Based on these changes, the role of the fragment size in the habitat use of *R. rattus* were interpreted. The order of different variables included in the model was founded on a spatial scale: the variables affecting the presence of *R. rattus* on the largest spatial scale were included first. Thus, the variables determining the habitat use of *R. rattus* on a metapopulation or population level were included in the model earlier than those operating more in an individual level. As the interpretation of EFRA rested on an existing ecological knowledge and the hypotheses under study, it guided the data analysis using the best of the author's ecological understanding and its limitations.

### 3.5. Morphological measurements and analysis

A total of 87 introduced and 62 nesomyine rodent specimens were measured for estimating probability for competition between introduced and nesomyine rodents based on morphological traits (IV). The data included representatives of all genera of the Nesomyinae except *Hypogeomys*, *Monticolomys*, and *Voalavo.* In total, data on 11 species of native Malagasy rodents was used.

However, data on the length of the head and body for most of these excluded species was obtained from the literature and used for comparison of size. Specimens of *R. rattus* were collected by J. T. Lehtonen in Ranomafana National Park between September and November 2000. The specimens of native Malagasy rodent were from the collections of the Museum of Natural History, London; Muséum National d.Histoire Naturelle, Paris; and the Finnish Museum of Natural History, Helsinki (collected during the field work of this thesis). Data on *Rattus norvegicus* and *Mus musculus* belongs to the Estonian specimens from the Zoological Museum of the University of Tartu, Estonia. The external and cranial proportions were assumed not differ significantly between European and Malagasy populations of the same species.

A total of 19 measurements were used in this study: 8 external, 4 skeletal, and 7 craniodental. They were selected from a larger number of characters based on a previous ecomorphological study (Miljutin 1997 and 1999). Cluster analysis (Sneath & Sokal 1973) was used for the estimation of similarity between species. Two procedures were made: 1) ranging of character values and 2) calculation of the Manhattan distances between species using unweighted pair-group average linkage.

## Box 1. Elaboration

From the viewpoint of complexity, ecology is very close to the social sciences (Pigliucci 2002, Hansson 2003). Interestingly, many social scientists and ecologists seem to rely on logistical regression models, but they use them in different ways. In social sciences, regression analysis is often supported with the analysis method called elaboration. Elaboration, which is more a way of thinking than a statistical method, studies the relationship between two variables in a context of several other variables. It allows causal inference in non-experimental research (Blalock 1961).

If it is observed that the variable X precedes Y and hence it would likely be concluded that X causes Y, it has to be proven that Y is not caused by some variable other than X. In experimental studies it is possible to use a control without X and treatment with X. If Y is observed only with X, the causality theorem is supported. However, it still has to be proven that Y can't occur without X.

Elaboration recognizes three situations which may occur to the original bivariate relationship (X,Y) with the introduction of a test variable (Z, Figure 1). Other variables (Z) can be excluded by standardizing them by means of models or by means of thinking experiments. If the standardizing of Z does not exclude a relation between X and Y, causality is supported. If the inclusion of Z removes the effect of X, it means that Z affects both X and Y and causes relation between them (explanation) or X affects Z which affects onward Y (interpretation). Also, Z may change a way in which X affects Y (specification). Of course, there are often more than three variables when the whole situation is much more complicated.

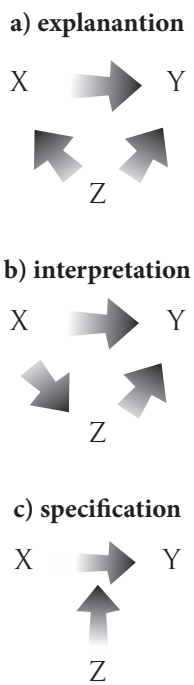



*Figure 1. Three analysis tools of elaboration*

## 4. Main results and discussion

### 4.1. Rodent species in Ranomafana area

A total 698 rodent individuals were captured in 6204 trap nights in 1996 and 1998–2000 (I, II, Table 1). Five endemic species (*Nesomys rufus*, *N. audeberti*, *Eliurus tanala*, *E. minor,* and *E. webbi*) and introduced *R. rattus* were found in both the secondary and the primary forests. The house mouse *M. musculus* was only found in the secondary forests. In addition to our regular trapping *Gymnuromys roberti* was captured twice in the secondary forest close to Miaranony village (Map 1) in 1999. We didn't capture *Brachytarsomys albicauda* with traps but we observed it close to both Miaranony and Talatakely villages. *Brachyuromys betsileonsis* was absent from our data probably because our traps were not located above 1120 m a.s.l. In other studies, *B. betsileonsis* has been captured in RNP above 1200 m a.s.l. (Carleton and Schmidt 1990, W. Rakotonirina, per. comm.). Also *Monticolomys koopmani* has been observed in RNP (Soarimalala & Goodman 2011) but we could not capture it.

### 4.2. Effects of human disturbance on endemic rodent occurence

Although the total number of endemic rodents was higher in the primary forests than in the secondary forests, selective logging or other types of light forest disturbance doesn't seem to be a big threat to endemic rodent species in Ranomafana (I). None of the three most common native species (*Nesomys audeberti, N. rufus,* and *Eliurus tanala*) were more abundant in un-logged than in selectively logged forest (I, Figure 2). However, all other native species except *Eliurus tanala* were absent in secondary bushes (I). Thus, there is no doubt that deforestation contributes to the disappearance of most of the native rodent species. The same kind of result was found in the spiny forest in southern Madagascar where small mammal species diversity declined by 40 percent in response to clearing (Scott et al. 2005) and from Central China where small mammal diversity was higher in deforested than in afforested habitats (Raoul et al. 2008).

When we were studying the effects of forest fragmentation on rodents, the study fragments were at relatively low elevations (650–910 m) and presented only two common native species: *Eliurus webbi* and *Nesomys audeberti* (II). In our study area, *E. webbi* does not seem to be sensitive to forest fragmentation as its mean abundance per study grid was almost the same in every size class of fragments and in control sites (II, Figure 3). *N. audeberti* was virtually absent from the fragments although two or three individuals were trapped in each control site (II, Figure 3). In addition to fragmentation, *N. audeberti* probably suffers from rapid deforestation below 800 m in elevation where it used to be the most common. Dehgan (2003) studied the lemurs partly at the same fragments in RNP as us and found that lemur species richness could not be predicted by the size of forest fragments.

*Table 1. Number of individuals trapped for each species of rodent in six monitoring sites in secondary forest (SF) and in primary forest (PF) in 1996 and 1998–2000 (total trap-days accrued is shown in parentheses). Data of years 1996 and 1998 was used in Chapter I but data of years 1999 and 2000 are not shown in other chapters of the thesis.*

| Species | SF (272) -96 | -98 | -99 | -00 | PF (272) -96 | -98 | -99 | -00 |
|---|---|---|---|---|---|---|---|---|
| *Mus musculus* | 2 | 3 | 5 | 1 | - | - | - | - |
| *Rattus rattus* | 30 | 30 | 40 | 17 | - | 1 | 6 | 1 |
| *Eliurus minor* | 1 | 1 | - | - | 2 | - | - | - |
| *Eliurus tanala* | 1 | 6 | 3 | 6 | 8 | 7 | 8 | 3 |
| *Eliurus webbi* | - | 1 | 3 | 1 | 1 | 1 | 1 | 1 |
| *Nesomys audeberti* | - | 10 | 11 | 4 | 2 | 2 | 2 | 4 |
| *Nesomys rufus* | 7 | 3 | 1 | 1 | 8 | 24 | 19 | 12 |
| Total rodents | 41 | 54 | 63 | 30 | 21 | 34 | 36 | 21 |
| Tolal nesomyines | 9 | 21 | 18 | 12 | 21 | 33 | 30 | 20 |

Contrary to our results, *E. webbi* was found only in fragments larger than 28 hectars in the littoral forest of southeastern Madagascar (Ramanamanjato & Ganzhorn 2001). The fragments in Ranomafana were much younger than in the littoral forest. It is possible that all negative effects of isolation are not yet seen in Ranomafana, and the native rodent populations suffer from extinction debt (Tilman et al. 1994, Hanski & Ovaskainen 2002). In the dry deciduous forest of western Madagascar, the abundance of endemic rodents decreased as forest fragments became smaller (Ganzhorn 2003). In the Amazonian forest, small mammal abundance and species diversity were not affected by forest fragment size but rather by the quality of the open-habitat matrix (Santos-Vilho et al. 2012). It is not surprising that the response to forest fragmentation varies from species to species and from region to region. As shown in our methodological study (III), the effect of forest fragmentation is a very complicated phenomenon. There can be many other habitat variables which may effect via the fragment size. However, the situation is different with endemic rodents than with *R. rattus* because the forest fragments are really habitat fragments for most of the endemic rodent species but not for *R. rattus* (II, III).

### 4.3. Occurence of black rat in Ranomafana area

The abundance of *R. rattus* increased with increasing forest disturbance and it was most common in heavily logged secondary forest (Figure 2). Therefore, *R. rattus* benefits from deforestation unlike endemic rodents. However, *R.rattus* can survive also in primary forests in eastern Madagascar (Goodman and Carleton 1996, 1998). We observed *R. rattus* the first time in selectively logged primary forest areas in Ranomafana in 1998 (I). Later it has been captured also in un-logged forest areas in Valohoaka in 1999, 2000 (Table 1), and 2012 by the students of a tropical field ecology course (L. Sandholm. pers. comm.). In Chapter I we said that *R. rattus* was never captured farther than 500 meters away from human habitation or permanent satellite camp-sites. The distance from Valohoaka to the nearest field is about 1800 meters but there is also a small satellite campsite which was used temporarily in 1999–2000 and in 2012. It is difficult to say if the temporarily used campsite and its exposed garbage pit are the only things attracting *R. rattus* there.

By means of the best-fit logistic regression model probability, of *R. rattus*'s presence increased with decreasing canopy cover, distance from forest edge, and from human habitation, and with increasing herbaceous cover, altitude, and overstory tree height (I). All these variables are in line with the suggestion that the occurrence of species is associated with forest disturbance. However, in the third chapter (III) we express our concern on the suitability of best-fit models to explain ecological phenomena. Mac Nally (2000) highlighted that the best-fit procedure can be appropiate when the

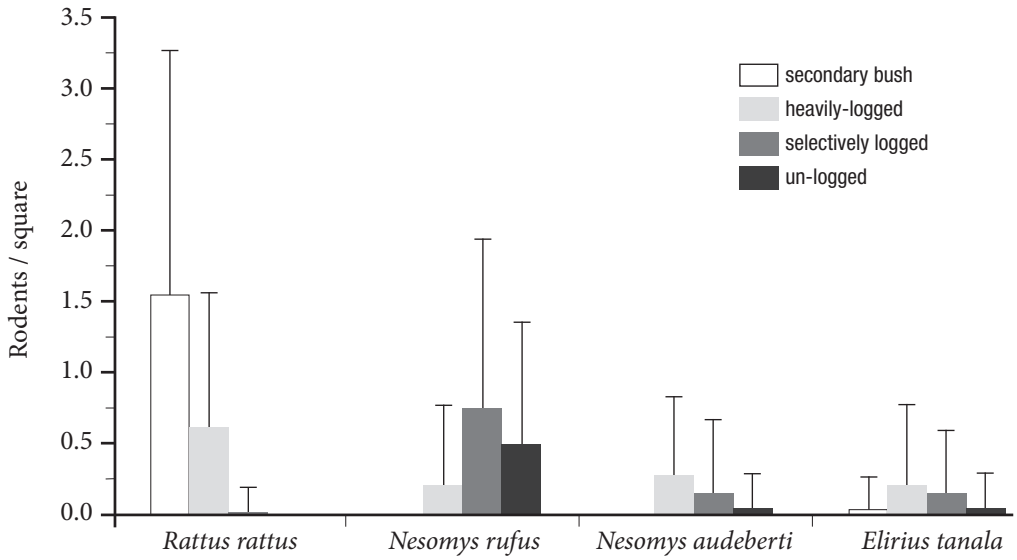



*Figure 2. The mean abundance of different rodent species per trapping square in different categories of natural state in RNP (I).*

purpose of the modelling is to achieve a 'predictive' model, but it shouldn't be used it for explaining causality.

Because our first results suggested that the spread of *R. rattus* is associated with deforestation it was interesting to also study the effects of fragmentation on the occurrence of *R. rattus.* The abundance of *R. rattus* was higher in the fragments than in continuous forest, but the difference was not statistically significant (Figure 3, II). The size of fragment was also not significantly correlated with the abundance of *R. rattus* (II). Similar results were found in the littoral forest of southeastern Madagascar (Ramanamanjato and Ganzhorn 2001), but in the dry deciduous forest, the capture rate of *R. rattus* was negatively correlated with the fragment size (Ganzhorn 2003).

The above-mentioned best-fit logistic regression model could not predict the presence of *R. rattus* in fragmented areas well (II). When we were analysing the habitat data in fragmented areas, we tried to better understand what ecological factors determine the presence of *R. rattus* by using the EFRA approach (explanatory framework based regression analysis, III). We demonstrated the sensitivity of the size of fragment to other variables in the regression models (Figure 4). The dramatic variation of the coefficient of fragment size was not surprising when remembering that *R. rattus* utilizes open areas, too. A forest fragment does not necessarily mark the limits of a habitat fragment for this species and that is why its role in the habitat models of rat is fragile. It may also explain the difference in results about the correlation between the fragment size and the trapping rate of *R.rattus* in different areas in Madagascar.

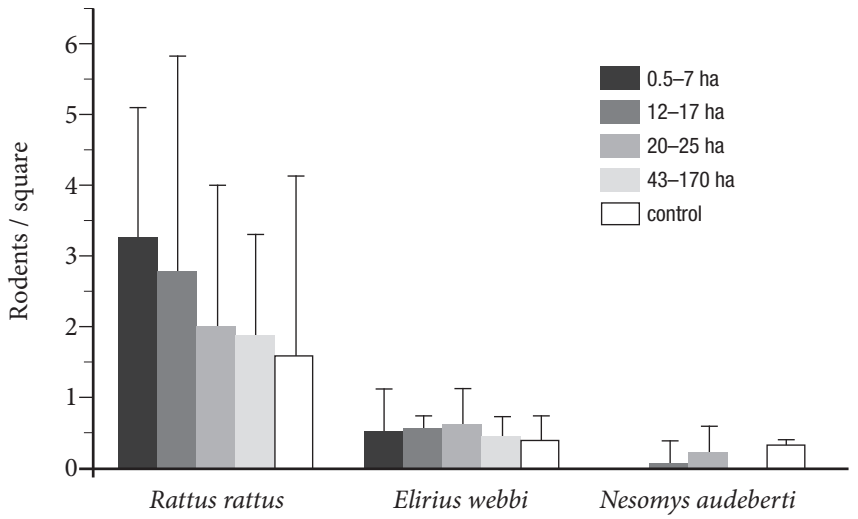



*Figure 3. Mean number of rodents captured per square and standard deviations in different size categories of fragments. The values were calculated from mean number of rodents per square of each fragment (II).*

The assocation between the size of the fragment and other variables varies in different areas. The measured value of the size of the fragment can rather be viewed as an index capturing certain features of the forest fragment (III).

In our data especially two habitat variables had a dominant role: 1) distance from a field which may be connected to the food resources of the rat and 2) liana stem density which can be seen as an indicator of the virginity of forest (III). Food resources provided by fields and all kind of forest structure changes reflecting human presence are probably more important to *R. rattus* than the size or shape of the forest fragment.

### 4.4. Interaction between black rat and endemic rodents

Based on a comparison of body size, body construction, and craniodental characters it is probable that nesomyine rodents compete with *Rattus rattus* but not with *Rattus norwegicus* (IV). The probability of interspecific competition was estimated as:
1) very high between *R. rattus* and *Gymnuromys roberti*;

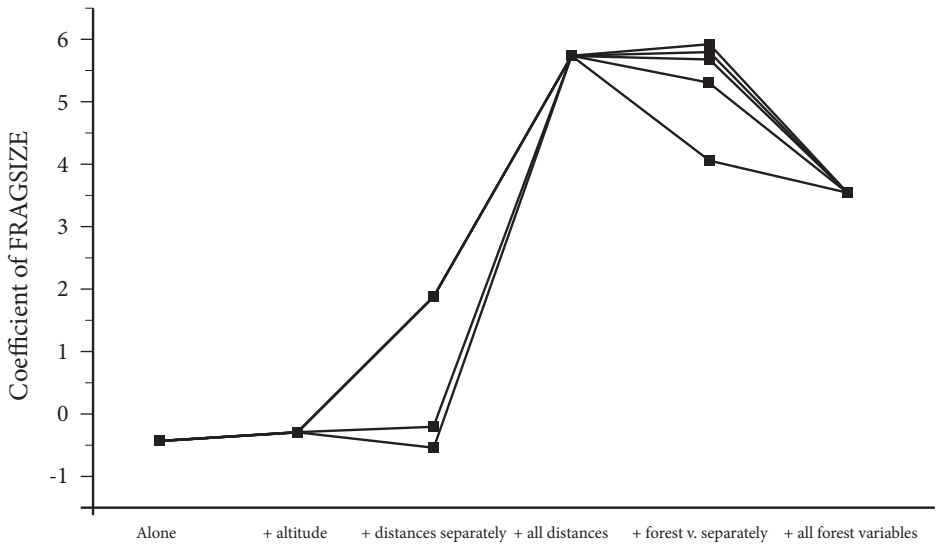



*Figure 1. The coefficients of* FRAGSIZE *in models that are organized according to the operational level explanatory framework (see text). Horizontal axis shows the inclusion order of the variables into the logit-model, the vertical – coefficient of* FRAGSIZE *in the corresponding model. The effects of separate inclusion of variables in the distance and forest structure packages are represented as well. The exact values of the coefficients and their p-values are given in Table 2. The straight lines connecting the different models are just to make comparison of changes easier. It is by no means meant to indicate linearity of change between the models.*

2) high between *R. rattus* and species of *Nesomys* and larger semiarboreal *Eliurus* (*E. tanala*, *E. webbi*);
3) moderately low between *R. rattus* and *Brachytarsomys albicauda* and larger species of arboreal *Eliurus* (e.g. *E. myoxinus*); and
4) low between *R. rattus* and species of *Brachyuromys* and *Macrotarsomys ingens*.

Other native Malagasy rodents than those mentioned above and the introduced rodents likely do not compete with each other, except maybe for *M. musculus* and the poorly studied *Monticolomys koopmani* and *Voalavo gymnocaudatus.*

Although Goodman and Sterling (1996) demonstrated that food preference of *R. rattus* overlaps with *Brachyuromys ramirohitra, Eliurus tanala, E. webbi, Gymnuromys roberti,* and *Nesomys rufus,* there are no other experimental studies testing the competition hypothesis between the black rat and Nesomyine rodents. In Madagascar, *R. rattus* is largely terrestrial and uses the same kind of ground burrow types as *G. roberti* and *N. rufus* (Laakkonen et al. 2003). In future studies, particular attention should be paid to species-pairs *R. rattus – Gymnuromys roberti* and *R. rattus – Nesomys rufus.* It is possible that the populations of *G. roberti* have already dimishned in RNP. During four years of trapping it was observed only twice close by Miaranony village in RNP. Previously *G. roberti* has been reported in RNP close to Talatakely village, which is the most intensively studied area in RNP (Carleton & Schmidt 1990). *G. roberti* is very abundant in the Andringitra National Park which is connected with RNP by a forest corridor (Goodman & Carleton 1996).

Interactions between *Eliurus webbi* and *Rattus rattus* could be worth studying in the future as well. Based on the fragmentation study in RNP (II), *E. webbi* may be more susceptible to competitive effects from *R. rattus* in fragments than in continuous forest although no negative correlations between capture rates of *R. rattus* and *Eliurus webbi* have been found in the littoral forest or in the dry deciduous forest (Ramanamajato & Ganzhorn 2001, and Ganzhorn 2003). In contrast, hardly any Nesomyine rodents were captured in fragments in the humid forests of Andranomay/ Ambohitantely where R. rattus was abundant (Ganzhorn et al. 2003). However, drawing conclusions about interspecific competition from correlation analyses should be treated with caution (Strong et al. 1984).

Among potential competitors with *R. rattus*, four species – *Brachyuromus albicauda, Brachyuromus villosa*, *Nesomys audeberti,* and *Nesomys lambertoni* – are on average larger than the black rat (IV). This larger size may help them to predominate over *R. rattus.* All other potential competitors with *R. rattus* are smaller or equal in size and may be threatened by the black rat.

When considering *R. rattus* in a global perspective, it has occupied a wide variety of habitats on islands without an extensive native fauna of small mammals (New Zealand, Hawaii, Puerto Rico, Galápagos islands, Timor, and numerous smaller islands), but where a diverse small-mammal fauna exists, black rats are usually absent or only small in numbers in undisturbed habitats (see Clark 1980, Aplin et. al. 2003). How-

ever, Madagascar is an exceptional case as *R. rattus* has invaded many different kinds of habitats with a rich native rodent fauna.

We recommend the ecomorphological approach (IV) for preliminary studies of recently described, extinct, and rare mammal species. Usually it is very difficult to get other kind of data about species which should be the focus of conservation studies. Dayan and Simberloff (1998) concluded that mammals have determinate growth, which makes them favorable for morphometric studies and that while many studies of invertebrates fail to confirm the hypothesis of interspecific competition, many studies of vertebrates do suggest its operation.

## 5. Final remark and future perspectives

This thesis suggests that deforestation and heavy logging promotes the spreading of introduced *Rattus rattus* in the humid forest of Madagascar (I). The forest fragmentation does not directly affect the occurrence of *Rattus rattus* but it may intensify negative association between *R. rattus* and endemic rodents (II, III). Therefore, forest fragmentation can be problematic for the Malagasy rodent community.

For native Malagasy rodents, clear-cutting is disastrous and forest fragmention may have a diminishing effect on populations of some species, e.g. *Nesomys audeberti* (I,II). The forest below 800 m in elevation where *N. audeberti* is most frequently documented is rapidly disappearing in the Ranomafana-Andringitra corridor area. Many other forest-dwelling animal and plant species may suffer from the same problem. Accordingly, it is important to ensure forest protection at different elevations.

The interspecific competition between *Rattus rattus* and morphological similar native rodent species (e.g. *Gymnuromys roberti*) will be an important topic to study in the future. One possibility to study it is via removal experiments. In response to *R. rattus* removal, the populations of the Australian native rodents increased due to immigration, juvenile recruitment, and increases in residency of females (Stokes et al. 2009). Other fruitful ways to study interspecific association could be a research on the effects of competition on individuals' fitness and physiological costs (Eccard and Ylönen 2003).

In the beginning of the thesis, it was discussed that invasive species drive native animal species to extinction more often by spreading parasites or pathogens or by predation than by competition. So far, there is evidence that some parasites are shared between *R. rattus* and nesomyine rodents, but there is no evidence that populations of native rodents suffer from those parasites (see Ganzhorn 2003, Laakkonen et al. 2003). We have also studied helminths of Malagasy rodents, but we found only one parasite species from endemic rodents (*Mastophorus muris* in *Eliurus tanala*) which is an endoparasite of *Rattus rattus* as well (Lehtonen et al. unpubl.).

One of the most potential pathogens that could spread from *Rattus rattus* to Nesomyine rodents is the plague. Duplantier and Duchemin (2003) mentioned the fol-

lowing case from Moramanga in 1932. Several specimens of *Brachytarsomys albicauda* invaded villages, later their bodies were found around houses and finally villagers came down with the plague. More parasitological and epidemiological studies are needed in Madagascar.

Moreover, it is important to start to study predator effects of introduced rodents on birds and other animals in Madagascar. It is an almost totally neglected research topic in Madagascar so far.

## 6. Acknowledgements

'*Tsara tsara kokoa miandry.*' This sentence, meaning 'It is better to wait,' was the first Malagasy sentence that I learnt. I am very sorry to everybody that I assimilated the sentence so completely in my dissertation process. First, I would like thank you all for your patience!

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